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PEMPHIGUS OBESINYMPHAE, A NEW AMERICAN APHID SPECIES WITH DEFENDERS AND SWOLLEN NYMPHS (HOMOPTERA: APHIDOIDEA: PEMPHIGIDAE)

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Abstract.—*Pemphigus obesinymphae,* n. sp., which is closely allied to *P. populitransversus* Riley, was discovered in Arizona and Utah and is described here. The new species forms galls on leaf petioles of *Populus fremontii* Watson, and produces 1st instar nymphs that possess heavy sclerotization and stout legs. The 2nd and 3rd instar nymphs are swollen and look superficially like wingless adults. The fundatrix, the 1st instar, 2nd instar and adult (alate) fundatrigeniae, the 1st instar exule deposited by the alate, the sexupara, and the gall are described. The differences found between the new species and the most similar previously described species, *P. populitransversus* and *P. knowltoni* Stroyan, are given.

The genus *Pemphigus* (Homoptera: Aphidoidea: Pemphigidae) contains about 65 species and is distributed throughout the northern hemisphere (Blackman and Eastop, 1984). All holocyclic species of *Pemphigus* form distinctive galls on cottonwood or poplar trees (the genus *Populus*). Lange (1965) reviewed what was known of the North American species of *Pemphigus.*

Most species of Pemphigidae (including Eriosomatinae, Pemphiginae, and Fordinae, as in Heie (1980)) show seasonal alternation of host plants. In this type of life cycle, the sexual phase, sexually produced eggs, and first parthenogenetic generations occur on the "primary" host, almost always a woody plant in a taxon that is characteristic for the aphid tribe or subtribe. Migrants from the primary host colonize the secondary hosts, where a series of parthenogenetic generations occurs. Related aphid species often have completely unrelated secondary host-plants; frequently these are herbaceous. Usually the primary host is colonized in autumn and abandoned in spring, and secondary hosts are used in summer.

For example, in the most common *Pemphigus* life cycle, sexually produced eggs overwinter on bark of a species of *Populus* (the primary host-plant). In spring, these eggs hatch to give rise to females, called the fundatrices. These initiate formation of galls on newly developing leaves or shoots, then mature and reproduce parthenogenetically within the galls. Typically, all offspring of fundatrices (the fundatrigeniae) are winged parthenogenetic females that migrate to certain herbaceous plants (the secondary hosts), where they deposit all-female broods. These nymphs descend through soil crevices to the roots, where they feed, develop into wingless adults, and reproduce, again parthenogenetically. These and subsequent generations of wingless female on roots are called exules. A series of overlapping generations of exules continues on roots of the secondary hosts until autumn when alate sexuparae are produced. The sexuparae migrate back to cottonwood trees where they enter bark crevices and

produce the dwarf males and sexual females. Sexuales mate and each female deposits a single overwintering egg. The fundatrices hatch from these eggs the following spring, to initiate new galls, thus completing the cycle. In many instances, exule generations may continue on roots of secondary hosts through the winter and into the next season; such life cycles are termed anholocyclic. In *Pemphigus betae* Doane, single clones have been shown to produce both the specialized wingless morphs that overwinter on roots of secondary hosts as well as the sexuparae that fly back to the primary host-plants in autumn (Moran, 1991). Both root-overwintering morphs and sexuparae are induced by low temperature (Judge, 1967; Moran et al., 1993). The secondary hosts of many *Pemphigus* species are unknown (Lange, 1965). A few species of *Pemphigus,* including *P. monophagus* Maxson in North America, omit migration to the secondary host-plants and prolong the gall-dwelling phase on *Populus* (see Aoki and Kurosu, 1988).

In this paper, we describe *Pemphigus obesinymphae,* a new North American species that shows unusual features. First, the fundatrigeniae exhibit defensive behavior and morphology during the first instar. Second, these 1st instar nymphs develop into 2nd instar nymphs which are swollen and which resemble small wingless adults. Third, the life cycle is unusual in that migration from galls is delayed until late autumn, overwintering appears to occur only on secondary hosts, and return migration by sexuparae occurs in spring rather than autumn. Results of field and laboratory studies on the behavior and life cycle of *P. obesinymphae* are reported elsewhere (Moran, 1993).

Pemphigus obesinymphae, new species

Metrical data are indicated as mean and range, based on 10 mounted specimens each for the 1st instar, 2nd instar and adult fundatrigeniae and 5 specimens each for the fundatrix, 1st-instar exule, and sexupara. Measurements are in millimeters.

1. Adult fundatrix (apterous). Body length 3.6 (3.3–3.8). Antenna 4-segmented; segment III 0.136 (0.116–0.176) and IV 0.099 (0.096–0.108) + 0.018 (0.012–0.020) in length. Apical rostral segment 0.100 (0.098–0.102) long, without secondary setae. Second tarsal segment and femorotrochanter of hind leg 0.146 (0.142–0.158) and 0.57 (0.54–0.61) long, respectively. Shape and distribution of wax plates as is usual in *Pemphigus* species (e.g., *P. populitransversus, P. dorocola* Matsumura (Aoki, 1975). Eighth tergite with 15 (10–19) setae, genital plate with 37 (31–48) setae.

2. Fundatrigenia. Only two generations occur in the galls, the fundatrix and her offspring, the fundatrigeniae. All adult fundatrigeniae are winged. Immature fundatrigeniae can be divided into four instars, using the following key:

1. Antenna 4-segmented; empodial setae long and capitate ..... 1st instar
– Antenna more than 4-segmented; empodial setae short and pointed 2
2. Antenna 5-segmented; wing pad absent ..... 2nd instar
– Antenna 6-segmented; wing pad present 3
3. Wing pad small, not extending past 1st abdominal segment ..... 3rd instar
4. Wing pad large, extending past 3rd abdominal segment ..... 4th instar

Below we describe the 1st and 2nd instar nymphs and adult of the fundatrigenia. *First instar fundatrigenia* (Fig. 1a, b): Body 0.77 (0.68–0.88) long. Head and thoracic

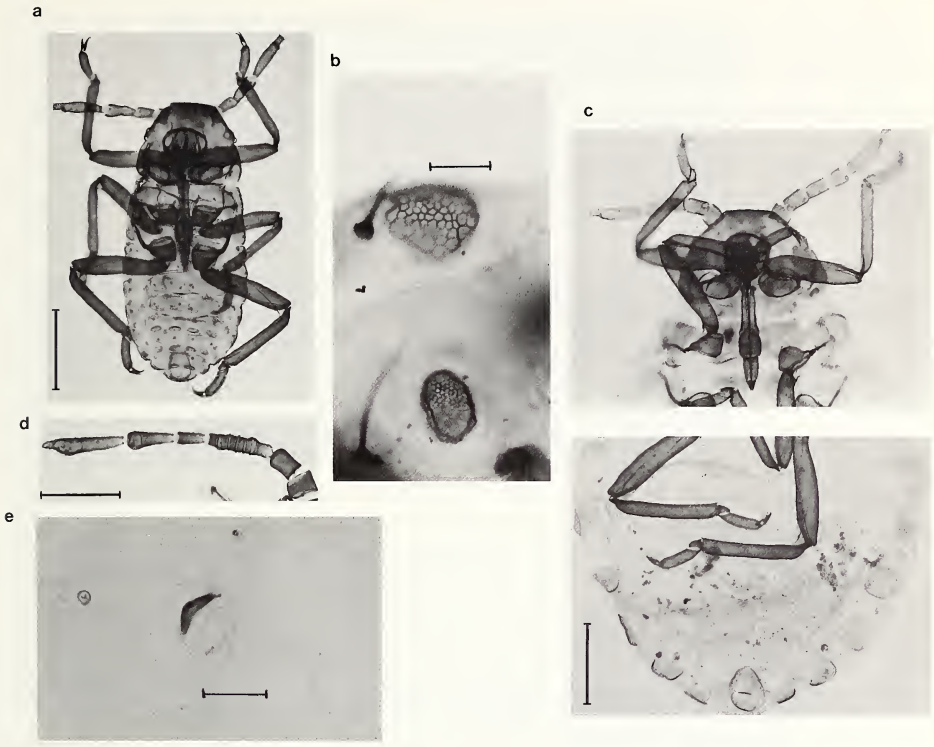

Fig. 1. Fundatrigenia of *Pemphigus obesinymphae*: (a) First instar nymph. Scale: 0.2 mm. (b) Wax plates of 1st instar nymph (pleural and marginal plates on 5th abdominal tergite). Scale: 0.02 mm. (c) Second instar nymph. Scale: 0.2 mm. (d) Adult antenna. Scale: 0.2 mm. (e) Adult cornicle. Scale: 0.02 mm.

tergites almost wholly sclerotized. Abdominal tergites I–VI each with a pair of marginal, oval or quadrate sclerites and a large transverse sclerite, which are well developed on anterior segments but reduced in size on posterior segments. Antenna 4-segmented; segments I, II, III and IV with 4, 2, 3 and 2 (base) + 5 (unguis) setae, respectively; longer basal setae on IV 0.010 (0.008–0.012). Length of each segment as follows: I: 0.045 (0.038–0.050), II: 0.051 (0.048–0.056), III: 0.080 (0.070–0.084), IV: 0.130 (0.108–0.138); III constricted at middle, sparsely spinose; IV spinose. Primary rhinaria ciliate, 0.009 (0.008–0.010) on III and 0.011 (0.010–0.012) on IV in axial length. Rostrum reaching hind coxae, at most extending a little beyond them; apical segment conical, 0.082 (0.074–0.088) long, without secondary setae. Head ventrally with a pair of thin setae between antennae, the longer one 0.039 (0.034–0.044) (N = 8). Legs well developed, fore and hind femorotrochanters 0.227 (0.196–0.240) and 0.263 (0.224–0.276) in length, respectively; second tarsal segment with 5 pairs of setae, 0.100 (0.080–0.106) long on hind leg; empodial setae capitate, extending beyond apices of claws. Abdominal tergites I–VI each with 3 pairs of long, pointed setae on sclerites; the longest seta on III 0.055 (0.044–0.064); VII with 2 or

3 pairs of setae; VIII with 2 (rarely 3) setae; cauda with a pair of setae; anal plate with 2 pairs of setae. Spinal and pleural pairs of wax plates (Fig. 1b) composed of distinct cells without "central kernel" (cf. Zwölfer, 1957), distinctly demarcated, located posterior to tergal setae, occurring on abdominal tergites V–VII, but pleural plates on VII at times absent (in that case, the number of setae on VII is also 2). Marginal pair of wax plates (Fig. 1b) also composed of distinct cells without "kernel," but not distinctly demarcated, located just behind marginal setae, occurring on abdominal tergites I–VII, but those on anterior segments usually indistinct. Cornicle ringlike.

Second instar fundatrigenia (Fig. 1c): Body 1.17 (0.98–1.32) long. Abdomen often swollen, 0.70 (0.48–0.93) wide. Ratio of abdomen width to body length 0.539 (0.440–0.631) for 34 specimens without the next instar cuticle developing inside (44% had the ratio larger than 0.55). Head and prothorax wholly sclerotized as in the 1st instar. Mesothoracic tergite with a large transverse sclerite mesially and a pair of sclerites marginally. Metathoracic tergite with a pair of sclerites mesially and a pair of small sclerites marginally. Abdominal tergites membranous, sometimes with small sclerites. Antenna 5-segmented; apical segment 0.115 (0.110–0.124) + 0.029 (0.024–0.034) long. Apical segment of rostrum 0.080 (0.076–0.084) long, without secondary setae. Femorotrochanter and 2nd tarsal segment of hind leg 0.297 (0.288–0.312) and 0.116 (0.112–0.122) in length, respectively. Empodial setae short and pointed. Abdominal tergites with short setae, longest seta on tergite III 0.012 (0.010–0.014). Wax plates distinctly demarcated, composed of indistinct cells; marginal pair of plates on all thoracic tergites and abdominal tergites I–VII; spinal pair of VII (rarely spinal pair on VII are divided into 4); spinal and/or pleural small plates rarely appearing on other abdominal tergites. Cornicle ringlike.

Adult fundatrigenia (alate) (Figs. 1d, e, 3a): Body 2.2 (1.9–2.5) long, Antenna (Fig. 1d) 6-segmented, the flagellar segments together 0.58 (0.52–0.62); the length of each segment as follows: III: 0.162 (0.140–0.184), IV: 0.081 (0.076–0.088), V: 0.123 (0.108–0.132), VI: 0.182 (0.172–0.192) + 0.028 (0.020–0.036). Antennal segment III shorter than IV + V together, which are slightly shorter than or as long as VI. Primary rhinarium of V rather large and quadrate, 0.035 (0.026–0.040) in axial length; that of VI very large, 0.066 (0.056–0.080) in axial length. Antennal segment III with 3–6 secondary rhinaria, of which the most basal is 0.054 (0.044–0.066) from basal articulation of segment, distal or basal to the small tooth-like process near base; 0–1 (usually 0) secondary rhinaria on IV and V, 0 on VI. Secondary rhinaria normal in type, extending at most round a fraction more than half the circumference of segment III; rarely 2 adjoining rhinaria forming a double-sized rhinarium. Setae at apex of antennal segment V maximally 0.012 (0.010–0.014) long, about 0.38–0.64 as long as basal articular diameter of V. Apical segment of rostrum 0.092 (0.088–0.096) long, without secondary setae, approximately about ½ as long as 2nd segment of hind tarsus. Small oval to transversely elongate spinal wax plates on abdominal tergites I–VI and a large elongate one on VIII, but plates on posterior tergites (except on VIII) reduced in size and often disappearing. Cornicle ringlike; only half of the "ring" sclerotized. Eighth tergite with 5 (4–7) setae; genital plate with 33 (29–37) setae. Second segment of hind tarsus 0.183 (0.174–0.196) long.

3. First instar exule (Fig. 2a). The exule nymphs are deposited by the fundatrigenia. Body length 0.51 (0.48–0.56). Antenna 4-segmented; segments I, II, III and IV with

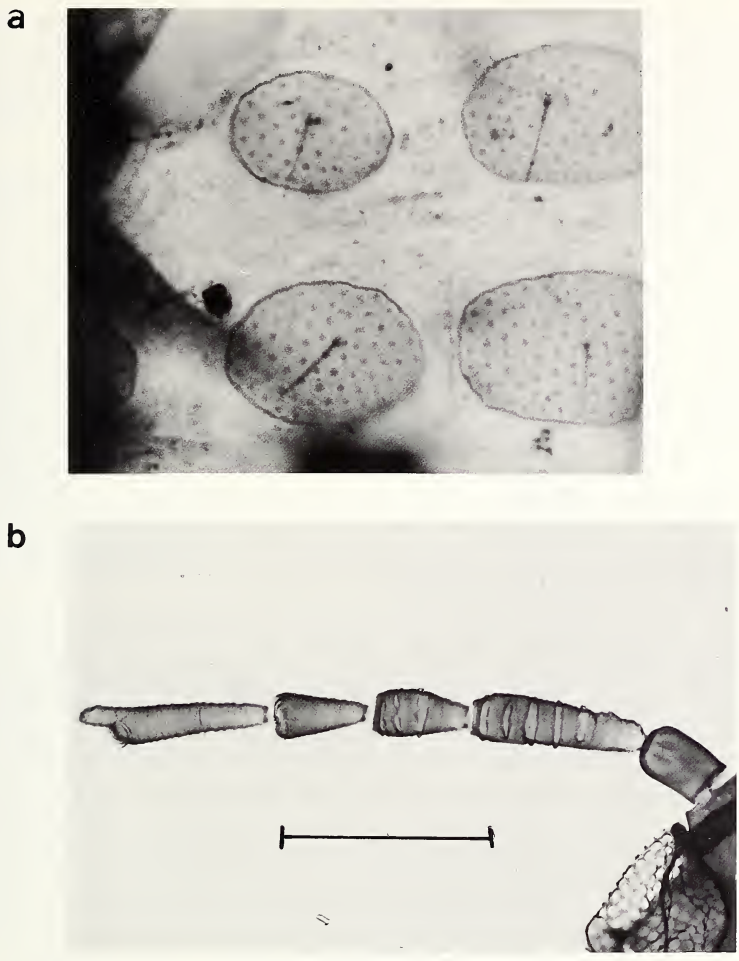

Fig. 2. (a) Wax plates of 1st instar exule of *Pemphigus obesinymphae* (spinal and pleural plates on 3rd and 4th abdominal tergites). Scale: 0.02 mm. (b) Antenna of adult sexupara of *Pemphigus obesinymphae*. Scale: 0.2 mm.

4, 2, 3 and 2 (base) + 5 (unguis) setae, respectively; longer basal setae on IV 0.016 (0.014–0.018). Length of each segment as follows: I: 0.038 (0.036–0.038), II: 0.040 (0.040–0.042), III: 0.041 (0.040–0.042), IV: 0.072 (0.070–0.074). Segments III and IV weakly spinose. Primary rhinaria fringed with distinct cilia, ca. 0.008 on III and 0.012 (0.010–0.016) on IV in axial length. Rostrum extending beyond hind coxae, but not reaching wax plates on abdominal tergite III; apical segment 0.064 (0.062–0.066) long, without secondary setae. Apical setae on tibia similar to others on tibia. Second tarsal segment with 5 pairs of setae, 0.059 (0.056–0.064) long on hind leg; empodial setae pointed, not reaching the apices of claws, 0.013 (0.012–0.014) long on hind tarsus. Hind femorotrochanter 0.148 (0.144–0.152) long. Abdominal tergites

I–VI each with 3 pairs of setae, VII with 2 pairs of setae, VIII and cauda each with a pair of setae, anal plate with 2 pairs of setae; longest seta on tergite III ca. 0.014. Wax plates distinctly bordered, composed of separated round cells each with a central kernel; a tergal seta occurring on each plate. Spinal plates on abdominal tergites III–VII, pleural ones on III–VI. Cornicle absent.

4. Adult sexupara (alate) (Fig. 2b). Body 2.0 (1.8–2.1) long. Antenna 6-segmented, the flagellar segments together 0.53 (0.49–0.57); the length of each segment as follows: III: 0.178 (0.156–0.192), IV: 0.089 (0.080–0.096), V: 0.095 (0.088–0.104), VI: 0.141 (0.132–0.152) + 0.031 (0.028–0.032). Primary rhinarium normal in type, ciliated, 0.018 (0.014–0.024) on V and 0.018 (0.016–0.020) on VI in axial length. Antennal segment III with 5–9 secondary rhinaria (mode 6), of which the most basal is 0.060 (0.054–0.066) from basal articulation of segment; number of secondary rhinaria on IV 2–3 and on V and VI 0. Secondary rhinaria slender, not fringed with cilia, extending round a fraction less than half the circumference of segment. Setae at apex of antennal segment V maximally 0.013 (0.012–0.014) long; basal articular diameter of V 0.016 (0.014–0.016). Apical segment of rostrum 0.090 (0.082–0.098) long, without secondary setae. Small oval to transversely elongate spinal wax plates on abdominal tergites I–V and a large on VIII, but plates on IV and V often faint. Cornicle absent. Eighth tergite with 4 or 5 setae; genital plate with 21 (20–22) setae. Second segment of hind tarsus 0.173 (0.164–0.184) long.

5. Gall (Fig. 3d). The galls are formed on the petioles of late flushing leaves; most are adjacent to the leaf blade. The shape is roughly spherical, with the lips of the gall slit sometimes bulging outward. Diameters of mature galls ranged from 8 to 16 (mean 13.8). Walls of mature galls are approximately 1.5 thick. The gall slit is irregular in shape and extends along the equator of the gall for about ⅓ of the circumference, with the petiole and leaf blade at the poles. The lips remain closed along most of their length until the emergence of the adult fundatrigeniae. However, each gall has a single, round ostiole, 1.2 in diameter; this may occur anywhere along the slit.

Material examined: All collections of *P. obesinymphae* were from petiole galls on *Populus fremontii* Watson in Arizona and Utah, USA, and were taken between 15 July 1991 and 31 July 1992. Arizona locations include: Santa Cruz County: Sonoita, Canelo (Audubon Research Ranch), Patagonia; Cochise County: Portal (Southwest Field Station); Graham County: Thatcher; Pima County: Tucson (Molino Basin, Santa Catalina Mtns.). The Utah localities include Salt Lake County: Salt Lake City (City Creek Canyon) and Davis County: Uintah (Weber River). Some alates that emerged from galls were confined in vials, and their 1st instar offspring were obtained.

The holotype is an alate fundatrigenia, containing embryos, collected from *Populus fremontii* by N. A. Moran at Patagonia on 13 October 1991. The paratypes are two adult fundatrices collected at Patagonia on 13 October 1991, two fundatrices collected at Patagonia on 8 September 1991 and 19 October 1991, one fundatrix collected at Portal on 16 September 1991, five emigrants collected at Patagonia on 25 August 1991, six emigrants collected at Patagonia on 13 October 1991, ten 1st instar fundatrigeniae, 14 2nd instar fundatrigeniae, and one 3rd instar fundatrigenia collected at Patagonia on 13 October 1991, and 12 1st instar exules deposited by emigrants collected at Patagonia on 25 August 1991. All the paratypes were collected from *P. fremontii* by N. A. Moran. The holotype and eight paratypes will be deposited in the U. S. National Museum, Beltsville, Maryland, U.S.A. An additional 16 paratypes

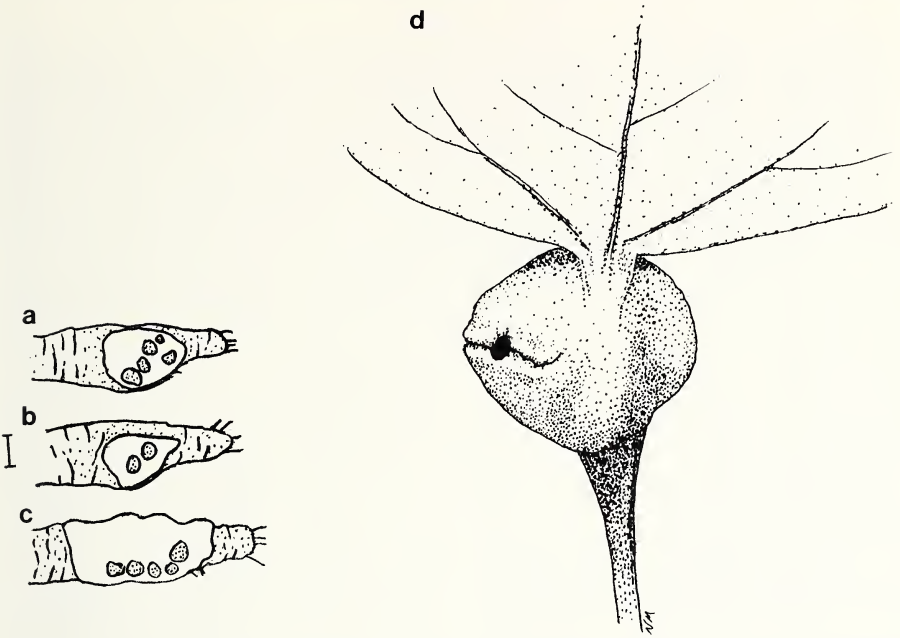

Fig. 3. Primary rhinarium on antennal segment VI of fundatrigenia of (a) *Pemphigus obesinymphae,* (b) *Pemphigus populitransversus,* (c) *Pemphigus knowltoni.* Scale: 0.02 mm. (b and c drawn from Stroyan, 1970). (d) Gall of *Pemphigus obesinymphae* on *Populus fremontii.*

will be deposited at the British Museum of Natural History, London and the Canadian National Museum.

Materials of *P. populitransversus* Riley used for comparison were taken from two galls preserved in alcohol; these had been collected by Roy Danielsson from *Populus deltoides* Marsh at Long Point, Ontario, Canada on 16 July 1986.

DISCUSSION

Taxonomy

Pemphigus obesinymphae, n. sp. is closely related to *Pemphigus knowltoni* Stroyan and, especially, to *Pemphigus populitransversus* Riley. These species can be easily distinguished from the other known gall-forming *Pemphigus* species because the adult fundatrigeniae of all three species have a huge primary rhinarium on the last antennal segment (Stroyan, 1970; Palmer, 1952; Fig. 3a–c). We hypothesize that the three constitute a monophyletic species group within the genus *Pemphigus.* Both *P. obesinymphae* and *P. populitransversus* form galls only on *Populus fremontii,* whereas *P. knowltoni* uses only *Populus angustifolia.* The three species differ in antennal morphology in the adult fundatrigeniae (Table 1). When adult fundatrigeniae are not present, the presence of a gall ostiole and morphological features of the 1st and 2nd instar fundatrigeniae can be used in order to distinguish *P. obesinymphae* and *P. populitransversus* in galls on *Populus fremontii* (Table 1).

Table 1. Comparison of features of *Pemphigus obesinymphae, Pemphigus populitransversus,* and *Pemphigus knowltoni.*

	Pemphigus sp.		
	obesinymphae	*populitransversus*	*knowltoni*
Reported geographic range	AZ, UT (likely in NM, CO, northern Mexico)	throughout eastern and western North America	UT (possibly in ID, CO, WY, MT)
Primary host	*P. fremontii*	*P. fremontii*	*P. angustifolia*
Gall position on leaf	petioles, near blade	leaf petioles, often at center	leaf blades, along mid-rib
Leaves used	late flushing leaves	first flush leaves	*
Ostiole	present	absent	*
Life cycle			
Sexuparae colonize primary hosts	spring	autumn	autumn
Overwintering	only on secondary hosts	as eggs on primary hosts	as eggs on primary hosts
Type of leaves galled	late flush	first flush	first flush
Fundatrigenia mature in galls	autumn	summer	summer
Secondary host taxa	unknown	various Brassicaceae	unknown
Adult fundatrigeniae			
Relative lengths of ant. seg. III & VI	III < VI	III ≥ VI	III ≥ VI
# secondary rhinaria on III	3–6	2–5	3–9
# secondary rhinaria on IV	0 (usually)–1	0–1	1–3
Rostrum length of embryos within adult fundatrigeniae	beyond 1st segment of fore tarsi, near bases of claws	not beyond 1st segment of fore tarsi	*
1st instar fundatrigeniae			
Abdominal tergites	heavily sclerotized	weakly sclerotized	*
No. setae on anal plate	4	5–6	*
Pleural & spinal pairs of wax plates on abd. tergites IV	absent	often present	*
2nd instar fundatrigeniae			
Body shape	swollen	slender	*
Pleural & spinal pairs of wax plates on abd. tergites IV–VI	none	well-developed	*

* Not observed.

Biology

The galls of *P. obesinymphae* contained aphids of only two generations: the fundatrix and fundatrigeniae, as is typical of *Pemphigus.* No apterous fundatrigeniae were found in galls of *obesinymphae,* although such forms are usual in both *Pemphigus spirothecae* Passerini and *Pemphigus monophagus* Maxson, other species that are known to have long-lived galls and defenders or suspected defenders (Aoki and Kurosu, 1986, 1988). The adult fundatrigeniae possessed embryos resembling typical *Pemphigus* exules. Therefore, this species probably alternates between two different host-plant taxa. Despite considerable searching and attempted transfers to several suspected plants (*Chenopodium* and *Poinsettia* species), its secondary hosts are yet unknown. The host alternation shows peculiar seasonal timing: fundatrigeniae fly from galls much later in the season than in other *Pemphigus,* overwintering occurs on secondary hosts, and sexuparae return to *P. fremontii* in May of the following year, after the first leaves have expanded. Sexuparae were collected from 5–20 May at Patagonia in 1992; they produced sexual offspring of typical appearance for the genus. Hatching fundatrices were collected from the same clusters of sexuales, suggesting that the eggs hatch within a short period rather than overwintering. Hatching fundatrices then establish galls on late flushing leaves; gall establishment was observed at the Patagonia site from 15 May–1 June 1992. The first fundatrigeniae began to be deposited in some galls on 10 June. This life cycle recalls that of *Schlechtendalia chinensis* (Bell), which also produces sexuparae in spring and which also has eggs that hatch without prolonged dormancy or overwintering (Takada, 1991).

P. obesinymphae exhibits four peculiar features: First, the life cycle is dramatically altered (Moran, 1993), with the result that galls occur only on the late leaves that expand later in the season as the shoots elongate. Most *Pemphigus* initiate galls on the early leaves; however, Bird et al. (1979) and Faith (1979) reported a dimorphism in the timing of gall initiation within *P. populitransversus,* with one gall type restricted to first flush leaves and a second restricted to late leaves. Second, 1st instar nymphs of the 2nd generation attack predators (Moran, 1993) and have the legs well developed and the tergites heavily sclerotized. Defensive 1st instar nymphs have been reported in *Pemphigus dorocola* (Aoki, 1978) and *P. spirothecae* (Aoki and Kurosu, 1986; Foster, 1990), but their tergites are not so strongly sclerotized as in *P. obesinymphae.* Third, galls have an ostiole, through which defenders enter and exit the gall (Moran, 1993). Ostioles are characteristic of galls of *Pemphigus dorocola* (Aoki, 1978) and *P. spirothecae* (Foster, 1990), but are not known from other American *Pemphigus.* Fourth, 2nd and 3rd instar nymphs of the 2nd generation are usually much swollen, and look as if they were wingless adults. Such swollen nymphs are not known from galls of any other *Pemphigus* species. Why they are so swollen remains to be investigated.

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